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Studies on Ecology and Behavior of Japanese Black Swallowtail Butterflies. III. Diurnal Tracking Behavior of Adults in Summer Generation

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The habitat preference of the black swallowtail butterflies (BSB), *Papilio helenus*, *P. protenor* and *P. memnon*, was studied by mark-release-and-'resight' method in Kodakasa-yama, Kochi, Japan. Flight behavior of BSB was little affected by this method. In *P. helenus*, males tended to prefer the edges of the forest instead of the treeless "gaps," though their population interchange between gap and edge was at the same low rate. Both the gaps and the forest interior were utilized for roosting. *P. protenor*, on the other hand, tended to remain in the gaps and the interior where they fed and oviposited. Thus, the daily flight trajectory of *P. protenor* seemed roughly opposite that of *P. helenus*. *P. memnon* which flies by soaring and gliding, preferred an open or edge area of the forest. Their host plants and nectar plants are different from those of the other two species and grow mainly in open areas. Thus, *P. protenor* and *P. memnon* are the more typical inhabitants of forests and open areas among the three BSB species.

INTRODUCTION

Marking has been generally believed to be the best method of studying mobil insects such as butterflies which have high flight activity. Some research on the population dynamics of swallowtail butterflies has been conducted utilizing this method (e.g., FALES, 1959; WATANABE, 1979b; KIRITANI et al., 1984). One of the fundamental requirements of the method is that it not affect the behavior of the butterflies marked. Repeated catches and releases of the same marked individual within one day would probably wound it, and might affect its subsequent life expectancy and behavior, as suggested by SINGER and WEDLAKE (1981). However, repeated observations of the marked butterflies without harmful effect to their flight behavior was possible by the "mark-and-resight" technique used in the present study. The daily flight range and activity pattern was studied in the black swallowtail butterflies (BSB), *Papilio helenus nicconicolens*, *P. protenor demetrius* and *P. memnon thunbergii*.

The BSB are commonly observed not only on hilltops but also in gaps and at the edges of a forest. Although few BSB females visit hilltops, many of them frequently visit the latter two sites where resource plants are available (Suzuki et al., 1985). In this investigation, the flight behavior of the BSB was studied by observing marked butterflies at several sites simultaneously. We also developed an analytical technique whereby the spatial activity patterns of the BSB were identified.

OBSERVATION SITES IN THE STUDY AREA

A detailed description of the study area, Kodakasa-yama, Kochi Prefecture, Shikoku, was given in Kiritani et al. (1984). Five primary observation sites and several subsidiary ones were selected within the study area to observe the site-visit behavior of BSB. One site was the interior of a forest, two were at gaps (small, sunlit, cleared forest areas) and two others were at edges (the periphery of the forest). Tall trees of *Zanthoxylum ailanthoides*, which is one of the hosts of *P. helenus* and *P. protenor*, grew mainly in the margins, but seedlings and young trees were prevalent in gaps. Nectar source plants, mainly *Clerodendron trichotomum*, grew sporadically throughout the study area.

The size of the sites varied from 10 m$\times$10 m to 30 m$\times$30 m. Data obtained from them were also used for estimating population parameters, and life tables of BSB were developed from the same sites (Watanabe et al., 1984).

METHODS

Before beginning simultaneous observation, the study area was repeatedly patrolled for two or three days. Adults of BSB (*P. helenus*, *P. protenor* and *P. memnon*) were captured in nets for marking, and the condition of their wings and sex were recorded before release.

The marking system that we used permitted us to distinguish 255 ($=2^8-1$) individuals by serial numbers, supported by the binary scale. Spots were put on the outside and/or the center of wings by a felt pen. For example, one spot on a respective area of the wing meant butterfly number 1 to 8, two spots there meant its number was from 9 to 36, three spots there meant its number was from 37 to 92 and so on (Fig. 1). Since rapid reading of the mark of a flying BSB was necessary in our method, marking was done in a silver color and the spots were large enough to be able to distinguish. Such marking

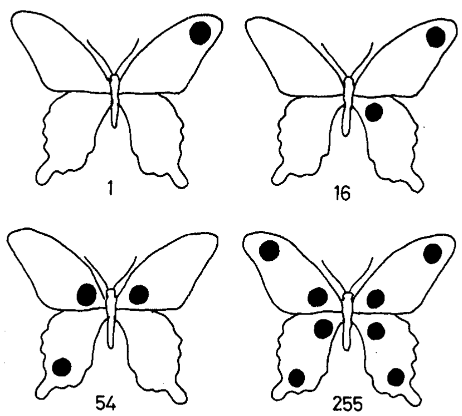

Fig. 1. The marking system supported by the binary scale.

procedure was considered to little affect the flight activity of BSB because most butterflies resumed normal flight when released. Butterflies wounded on the occasion of capture were discarded without marking.

The 'resight' was carried out at each observation site all day for two consecutive days in late August, 1980. Every marked BSB appearing in the sites was individually traced.

RESULTS

Sex ratio and population size

In the daytime, most adults of *P. helenus* and *P. protenor* roosted or flew slowly in the forest and the gaps (SUZUKI et al., 1985), while soaring and gliding flight from the margin to the open area was observed in *P. memnon*.

The total number of BSB marked in the study area were 113 males and 52 females in *P. helenus*, 129 males and 44 females in *P. protenor*, and 63 males and 13 females in *P. memnon*. Greater numbers of fresh young females compared to old ones were found in *P. helenus* ($0.05>p>0.01$), *P. protenor* ($0.05>p>0.01$) and *P. memnon* ($0.1>p>0.05$).

As already reported by SUZUKI et al. (1985), the pattern of female diurnal activity was different from that of the conspecific males. Males were predominant in all species in every study site (Table 1). Although the sex ratio observed in the margins seemed larger than that in the gaps, the hypothesis that there is no difference in the sex ratio between them has been disproved only in *P. memnon* ($F=15.419$, $p<0.005$).

Assuming that one resighting of any marked individual is equivalent to one recapture, population size of BSB was estimated by JOLLY's stochastic model (JOLLY, 1965). The mean daily number of BSB estimated in the study area (ca. 17.5 ha) was about 127 males and 150 females in *P. helenus*, 78 males and 48 females in *P. protenor*, and 23 males in *P. memnon*.

Hourly occurrence and persistency in observation sites

Figure 2 shows an example of the visiting frequency of males of *P. protenor* expressed in terms of daily two hour intervals at a site, K, located inside the forest. It can be seen that the flight activity was low in the morning but high in the afternoon. The visiting frequencies of BSB were analyzed by means of $\overset{*}{m}$–m relation (IWAO, 1968). The mean crowding ($\overset{*}{m}$) of visits at two-hour intervals was calculated for each BSB individual. Then the value of $\overset{*}{m}$ was related to the mean, m, for respective individuals. A single appearance of a BSB individual at each site in a two-hour interval results in $\alpha=0$. Individuals visited the site independently (Table 2). In *P. protenor* and *P. memnon*, the distribution of visits was contagious ($\beta>1$), meaning that the same butterfly visited the same site frequently within a particular time interval. Contrarily, the distribution of

Table 1. Daily sex ratios, ♀/(♂+♀), of BSB adults at different sites (±S.E.)

Sites[a]	S	O	G	Z	K
P. helenus	0.29±0.05	0.35±0.08	0.47±0.10	0.10±0.07	0.21±0.12
P. protenor	0.37±0.04	0.26±0.13	0.16±0.06	0.15±0.10	0.27±0.16
P. memnon	0.15±0.06	0.00	0.09±0.06	0.05±0.05	0.00

[a] S, O: margin of the forest, G, Z: gap of the forest and K: forest interior.

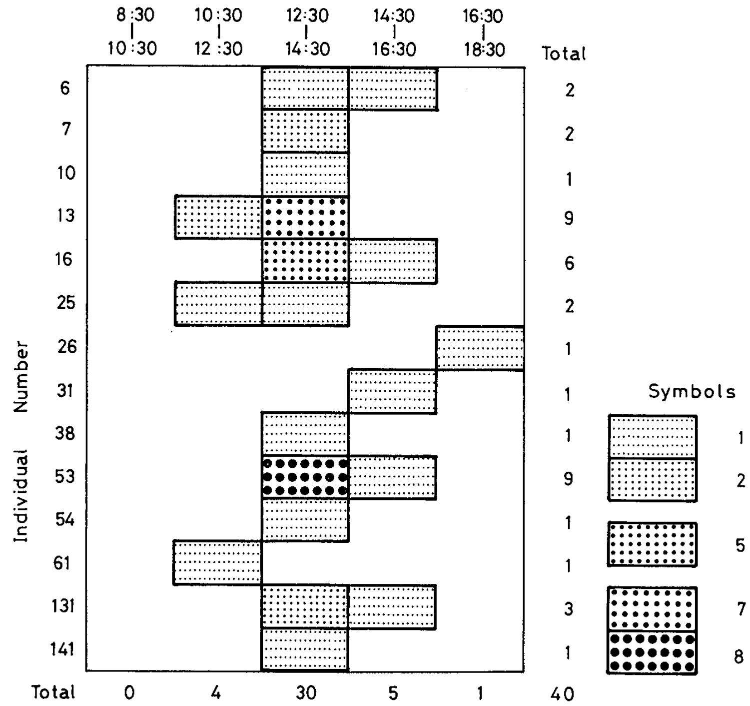

Fig. 2. An example of the appearance of male butterflies (*P. protenor*) at forest interior (K), August 24, 1980. Symbols indicate appearance frequencies during a two hour period.

Table 2. Distribution parameters for the number of hourly appearances of BSB

		Sites	α	β	r^2
P. helenus	Male	O	−0.1134	1.7557	0.70
		Z	0.4964	0.2863	0.02
		K	0.0288	0.5506	0.16
		K′	−0.0118	0.3730	0.37
	Female	Z	−0.1120	1.0291	0.19
P. protenor	Male	S	−0.3624	2.8207	0.73
		K	−0.2148	1.9735	0.97
		B	−0.4986	2.4121	0.82
		K′	0.0737	1.2819	0.90
	Female	—	—	—	—
P. memnon	Male	S	−0.1717	2.1348	0.94
		Z	−0.2000	1.5960	0.76
	Female	—	—	—	—

S, O: margins of the forest, Z, B: gaps of the forest, K, K′: forest interior, α: intercept on the m-axis, β: regression coefficient for the regression of mean crowding on mean density ($\overset{*}{m}=\alpha+\beta m$) based on the distribution per two hours, r^2: determination coefficient.

visits was roughly random ($\beta \leqq 1$) in *P. helenus*, though the determination coefficient (r^2) was quite low. The visits of *P. protenor* and *P. memnon* in mid-afternoon were higher than those in the morning; *P. helenus* did not follow this trend.

The frequency of sightings was recorded for individual butterflies in each site.

Table 3. Mean frequency of BSB visits to each site[a]

		No. of butterflies observed	Margin	Gap	Forest interior	
P. helenus	Male	32	0.419 ± 0.079	0.309 ± 0.071	0.271 ± 0.065	n.s.
	Female	6	0.500 ± 0.182	0.500 ± 0.182	0.000 ± 0.000	$0.05 > p > 0.01$
P. protenor	Male	19	0.186 ± 0.056	0.274 ± 0.083	0.540 ± 0.072	$p < 0.001$
	Female	7	0.460 ± 0.160	0.226 ± 0.087	0.314 ± 0.127	n.s.
P. memnon	Male	7	0.427 ± 0.160	0.510 ± 0.154	0.063 ± 0.048	$0.1 > p > 0.05$
	Female	0	—	—	—	—

[a] Frequency of visits is expressed as the ratio of the number of observations at the site to the total observations at all study sites within a day, viz. S/T. p-Values are calculated by using an analysis of variance in one-way classification.

Table 4. Emigration rate of BSB species between areas[a]

		No. observed	From gaps to margins	From margins to gaps	
P. helenus	Male	24	0.21	0.22	n.s.
	Female	5	0.33	0.00	—
P. protenor	Male	13	0.19	0.69	$p < 0.005$
	Female	4	0.30	0.33	—
P. memnon	Male	4	0.33	0.00	n.s.
	Female	0	—	—	—

[a] No. emigrants/(no. emigrants + no. sedentaries) in gaps and margins of the forests. p-Values are calculated using chi-square test in 2×2 contingency tables.

Here, T refers to the total number of sightings of a particular butterfly within a day at all observation sites and S is the number of visits by the same butterfly to a specific site. Frequency of visits by a particular individual at a given site is expressed as the ratio of S/T. If the butterfly is apt to return to the same site, the raito must be close to unity; theoretically, the ratio does not exceed unity. On the other hand, if most butterflies do not preferentially return to the same habitat, the ratio must become lower; that is, the ratio could be regarded as the index of persistency at the same habitat. The values of S/T ratio in the three kinds of habitats, margin, gap and the forest interior, for individuals of respective species were pooled and then averaged (Table 3). Males of *P. helenus* preferred margins, though the difference in the ratio between sites was not significant. Contrarily, males of *P. protenor* showed the highest persistency in the forest interior and the lowest in margins ($p < 0.001$). Females of both *P. helenus* and *P. protenor* seemed to prefer margins. Females of *P. helenus* and males of *P. memnon* did not appear to reside in the forest interior.

Population interchange between gap and margin

The S/T ratio shows how often a butterfly returns to the same site. The hourly rates of interchange of BSB between gap and margin are shown in Table 4. Males of *P. helenus* showed an equal degree of residency at both habitats. Twenty-one percent of the males observed at gaps flew to margins, and 22% of the males appearing in margins went to gaps. The remainder flew from gap to gap and from margin to margin, respectively. In *P. protenor*, the rate of males moving from margin to gap was significantly higher than that in the opposite direction. Males of *P. protenor* therefore were apt to either enter the forest or stay at the gaps. In *P. memnon*, contrarily, males tended to fly from gap to margin, so the habitat of this species seems to be an open area.

DISCUSSION

Marking technique

KIRITANI et al. (1984) estimated population parameters in summer generations of BSB males in the same area using the marking method. In the present study, the conspicuous silver spots on the wings permitted us to promptly read their individual numbers without disturbing their behavior. However, tracking the BSB for a long distance was practically impossible, partly due to their high flight activity and partly due to the dense vegetation in the study area. Instead, we made simultaneous observations at different observation sites throughout the daytime.

Based on the number of marked and unmarked butterflies observed at the sites, we were able to estimate the population parameters as reported by KIRITANI et al. (1984) for 1977–1979. The daily population size of males of *P. helenus* and *P. protenor* in 1980 was similar to those in 1977 but higher than those in 1978 and 1979. In addition, we were able to obtain estimates of the female population in 1980 by the resight method. This method was more practical than the conventional mark-and-recapture method when applied to a butterfly as large as BSB.

Although the method was very useful to estimate population size and to measure the persistency of butterflies, there were some limitations in its use for a population study. First, when a butterfly flew against the light we could not always identify its individual number accurately. Marked individuals were rapidly replaced by unmarked ones, partly due to emigration and death of the marked ones and partly due to immigration and recruitment of newly emerged adults to the population. Therefore, this method was available for only one or two weeks after intensive marking.

Habitat preference of the BSB

KIRITANI et al. (1984) studied the extent of population interchange of BSB males among three hilltops in the same area; however, few females visited these sites. In the present study a considerable number of females were observed at gaps and margins of the forest where their ovipositing and feeding plants were available.

Diurnal population interchange among the habitats is schematically shown in Fig. 3. *P. helenus* showed a tendency to remain at the margin while *P. protenor* preferred the gap. The gap thus tended to be visited repeatedly by the same *P. protenor* individual within a day. Males of *P. memnon* seemed to prefer gaps less; their flight trajectories were thus toward the open area during the day.

Flight trajectory has been studied in many butterflies, e.g., the black-veined white, *Aporia crataegi* (WATANABE, 1978), a yellow swallowtail butterfly, *P. xuthus* (WATANABE, 1979 a), an alpine checkerspot butterfly, *Euphydryas anicia* (WHITE, 1980), a small papilionid butterfly, *Luehdorfia japonica* (TSUBAKI and ITO, 1982) and so on. However, estimation of population size by the mark-release-and-resight method has been done in only

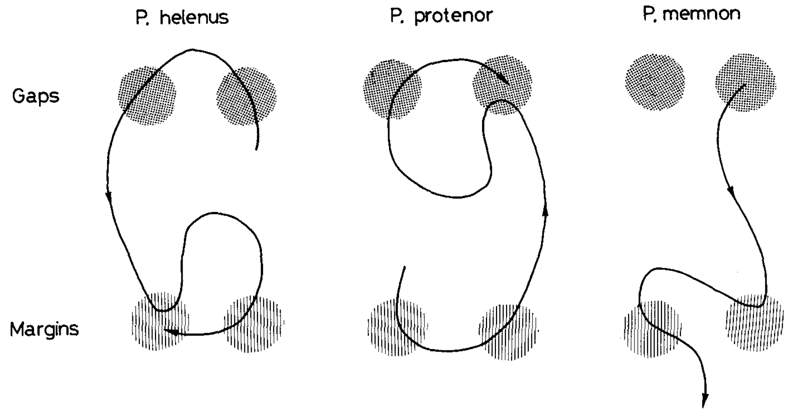

Fig. 3. A schematic representation of the flight trajectories of BSB among their habitats. Details are described in the text.

Table 5. Habitat attractiveness to BSB[a]

	Margin	Gap	Forest interior
P. helenus	+	+	±
P. protenor	—	±	+
P. memnon	+	±	—

[a] Intensities (+; ±; —) are based on Tables 3 and 4.

a few cases (e.g., LEDERHOUSE, 1982). Calculations of the index of persistency also indicated that the attractiveness of different sites differs by the species of BSB (Table 5). It should be pointed out that more BSB females feed on *C. trichotomum* grown in margins than in gaps. Fewer *P. helenus* were observed feeding on *C. trichotomum* in the gaps, however, *P. helenus* spent much time in the forest interior and the gaps (SUZUKI et al., 1985). They visited the margins repeatedly for a brief period in the evening, and, in addition, the females laid eggs on tall host trees there. As the darkness came on, they returned to the gaps or the interior to roost. In *P. protenor*, contrarily, gaps and the forest interior seemed an important habitat for their diurnal activities. In the afternoon, more *P. protenor* seemed to feed on *C. trichotomum* in the gaps where they stayed for a longer time. Although we did not find their mating site, the gap and the interior may be where copulation took place; the males may fly in to search for the females there. The margins were thus mainly exploited for feeding. *P. protenor* appears to inhabit the deepest forest among the three species of the BSB. For *P. memnon*, which seems to be a wandering species, gaps and the forest interior seem no more than roosting sites at night. As the darkness came on, they returned to the gaps or the interior from the open area. Neither gaps nor margins inhibit their high flight activity. In the present study, only one female returned to our study sites on a subsequent day, however, she was not found at the same site. Since their larval host plants were not *Zanthoxylum* spp. but cultivated *Citrus* spp., it may not be necessary for *P. memnon* to remain in the margins or gaps with *Z. ailanthoides*. This species also had no preference for *C. trichotomum* as its nectar source, but went from garden plants with large flowers to native plants with small flowers such as *Liriope graminifolia*, undergrowth of the forest.

The BSB inhabit semi-climax forests such as Kodakasa-yama, where the present study clarified that the daily habitat preference of the species differed. Therefore, simultaneous observation may have proven to be a useful tool for the study of sympatric species with high flight activities.

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